STROKE AMPLITUDE AS A FUNCTION OF AIR DENSITY IN THE FLIGHT OF DROSOPHILA

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With the accumulation of the necessary quantitative information, it is gradually becoming apparent that the complex wing movement of insects may represent the integration of several components, so interrelated that variation in any one is compensated precisely by appropriate changes in the others. Thus, for example, strong evidence in support of the theory that wingbeat frequency in the higher Diptera is regulated by the loading of the flight muscles has been put forward by Pringle (1949); in the case of Drosophila the relationship between frequency and atmospheric density agrees qualitatively with this point of view, emphasizing the fact that a major element of the load is the air resistance which the wings must overcome (Chadwick and Williams, 1949). Here, however, the observed changes in frequency were insufficient to compensate completely for the variation in load imposed by density change, indicating clearly that elements of the wing motion other than the frequency must also vary in an orderly manner if equilibrium is to be preserved.

From studies with vertebrate muscle (see Fenn, 1945), as well as from the few pertinent investigations with insects (Solf, 1931; Kraemer, 1932; Cremer, 1934), it is well known that not only the speed but also the extent of muscular shortening may be reduced by an increase in load. Regular changes in amplitude resulting from alteration in atmospheric density are therefore wholly to be expected. The problem in the present study has been the investigation of such changes from the viewpoint of their contribution to the integration of the flight mechanism as a whole.

One may reason, *a priori*, that in the analysis of insect flight the stroke amplitude should be as important as the frequency with which the wings are moved, since in theory the work done per beat is proportional approximately to the square of each of these factors. Evidence supporting this deduction has been produced, as far as frequency is concerned, by measuring respiration and rate of wingbeat concurrently during flights in which the level of activity was altered progressively by fatigue (Chadwick and Gilmour, 1940; Chadwick, 1947). However, such data suggest also that, unlike frequency, amplitude does not vary systematically under these experimental conditions, an inference which Williams (1941) has confirmed photographically.

It is well known, however, that in other circumstances amplitude may change considerably. Differences in the amplitude of right and left wings were observed by Voss (1914) and Stellwaag (1916), who discovered in this asymmetry the mechanism for steering in the horizontal plane. Moreover, Hollick (1940) has measured changes in the torque about the transverse axis which were dependent upon variation in the amplitude of both wings simultaneously, so that steering in the vertical plane also appears to be achieved through control of amplitude.

That variations in amplitude are not related solely to steering is attested by various other observations. Thus, Hollick (1940), like Magnan (1934), has described an inverse relationship between amplitude and the airspeed of the insect; while Sotavalta (1947) noted that smaller amplitudes are characteristic of insects flying freely in nature than of the same species when fastened, and that amplitude often increases when an insect carries a heavier load, as may be observed in predatory species with prey or in mosquitoes after a blood meal. Some of these facts may seem at first in contradiction with the decrease of amplitude noticed in fastened Drosophila at air densities above normal (Chadwick and Williams, 1949), but probably there is no real disagreement. If one makes the likely assumption that a fastened insect is already bearing a full load, any further burden on the muscles, as from an increase in the resistance of the air to the passage of the wings, can only result in a decrease in wingbeat frequency, amplitude, or both. A free-flying insect, on the other hand, ordinarily has some fraction of power in reserve. That the stroke amplitude of fastened Drosophila does in fact change systematically with alterations in air density is demonstrated by the observations described below.

Method

The experimental method was essentially that used previously by Hollick (1940) and Williams (1941), in which the envelope of the wing motion is recorded photographically by making a time exposure of a fastened insect in flight.

Females of *D. virilis* Sturtevant were anesthetized with carbon dioxide gas, and each specimen fastened to a wire by means of paraffin. The mount was then adjusted in a cylindrical holder which carried a retractable spring platform with which the feet of the fly were placed in contact, and the holder was slipped into the flight chamber, as shown in Figure 1. Care was taken to orient the insect so that flight was in a horizontal plane, with the specimen either head-on or sideways to the camera. Flight was induced by bringing a small permanent magnet, outside the chamber, into position beneath the platform.

The chamber consisted of a glass cylinder of heavy combustion tubing, 6 inches long and one inch in internal diameter, enclosed in a frame cut from stainless steel pipe. Threaded steel fittings provided for closure at both ends. As illustrated in Figure 1, one fitting carried inlet and outlet tubes for exchanging gas within the chamber; the other served to clamp a lucite flat, 0.25 inch thick, against the end which faced the camera.

Illumination was supplied by microscope lamps, one at either side of the chamber; these were turned on only while a record was being made. Exposure times of 1 to 2 seconds, aperture of f/11, gave head-on photographs at about 1 diameter on Super-XX film from which measurements of vertical amplitude could be made satisfactorily (Fig. 2). With the insect in side view, better pictures were obtained with an exposure of 0.2–0.5 second at aperture f/16 (Fig. 3).

Pressure within the chamber was varied by adding oxygen from a commercial cylinder, or by means of a vacuum pump. Positive pressures were read from a gauge, negative pressures from a mercury manometer against which the gauge had been calibrated up to a pressure of 3 atmospheres. Higher pressures were measured by gauge alone, assuming a linear extrapolation of the calibration data. The

atmosphere within the chamber was kept moist by evaporation from a piece of dampened filter paper. After each change of pressure a few minutes were allowed for equalization of the chamber with the laboratory temperature of 27 ± 1 degrees C.
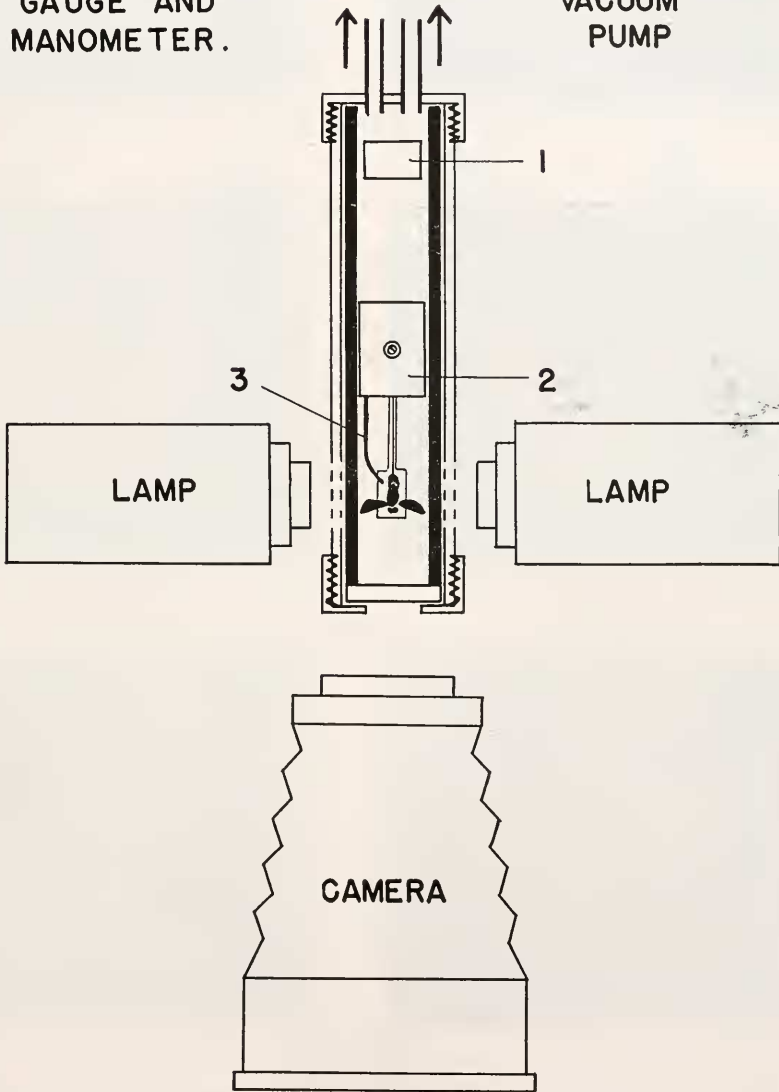

FIGURE 1. Diagram of apparatus. 1, piece of moistened filter paper; 2, holder for insect mounting and retractable platform; 3, stop for platform. For a description of other details, see text.

FIGURE 2. Representative series of head-on photographs to show alteration in stroke amplitude of a specimen of *D. virilis* in successive flights at different air pressures, as follows: a. 3863 mm. Hg; b. 2311 mm. Hg; c. 1520 mm. Hg; d. 760 mm. Hg; e. 380 mm. Hg; f. 190 mm. Hg. Records obtained at 3087 mm. Hg and at 95 mm. Hg have been omitted.

FIGURE 3. Series of silhouettes, traced from enlargements of original photographic records, to show changes in envelope of wing movement of a specimen of *D. virilis* during successive flights at different air pressures. Left lateral view. a. 3863 mm. Hg; b. 3087 mm. Hg; c. 2311 mm. Hg; d. 1520 mm. Hg; e. 760 mm. Hg; f. 380 mm. Hg; g. 190 mm. Hg; h. 95 mm. Hg.

TABLE I

D. virilis: vertical amplitude of wingbeat as a function of air pressure and density

Pressure in mm. Hg	3863	3087	2311	1520	760	380	190	95
Density in gm. per L.	5.97	4.76	3.56	2.34	1.16	0.57	0.28	0.13
Specimen Number	Stroke Amplitude in Degrees of Arc							
516–3	102	103	112	112	127	129	—	137
517–1	100	103	109	98	117	138	138	138
517–2	100	92	96	103	111	127	149	143
517–3	80	99	105	90	111	106	121	138
518–2	104	113	105	102	118	127	124	121
518–3	110	111	113	128	123	139	134	141
518–4	102	114	114	119	124	126	132	134
518–5	99	114	120	130	131	144	147	129
519–1	94	113	116	121	148	148	152	158
519–2	114	124	117	127	135	154	137	139
619–2	119	121	108	106	124	132	140	142
Average	103	110	110	113	124	133	138	138
Standard Error	±3.1	±2.9	±2.1	±4.1	±3.3	±3.9	±3.2	±2.8
Number of Observations	11	11	11	11	11	11	10	11

Flight was permitted only during the making of a record. Each insect was first studied at normal pressure, after which the same individual was tested over the series of positive and negative pressures shown in Table I. Ordinarily only one or two records were taken at each pressure. The data reported in the several tables represent average figures in all cases where more than one record was available.

In analyzing the photographs, each record was projected and traced at about 8 diameters. The apparent amplitude, in head-on view, was then read from the drawing with the aid of a protractor, as the angle between the two extreme positions of the anterior margin of the wing.

Because of foreshortening in pictures taken in lateral view, the apparent position of the wing in such records may differ appreciably from the true position. The latter was therefore determined by reconstruction before measurements were made, as follows (see Fig. 4):
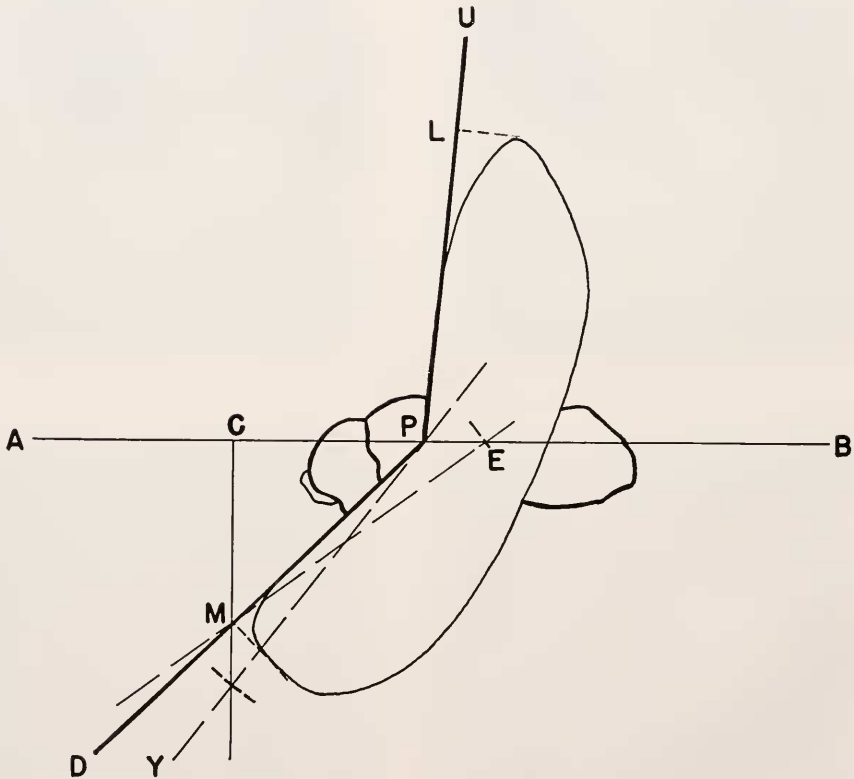

FIGURE 4. Diagram to show method of reconstructing from a photograph in side view the true angular displacement of the wing during the downstroke. For explanation, see text.

A horizontal line, AB, was drawn through the wing articulation, P, on the tracing; and extensions, UP and DP, of the costal margin in the extreme up and down positions were constructed. The true relative length of the wing, PL, was determined by dropping a perpendicular from the wingtip to UP in a record

of the same specimen taken at normal pressure, where it was known from head-on photographs that the costa is approximately in a vertical, parasagittal plane. The apparent length of the wing in the downstroke, PM, was similarly laid off; and a perpendicular, CM, drawn from M to AB. The true position of the costa in the downstroke was then found as the line connecting (1) P, and (2) the intersection of line CM with an arc of length PL centered at P. This reconstructed position of the costa is represented by the broken line, PY, in the figure.

Angles UPA and YPA were now recorded.

A similar reconstruction could be made for the position of the costa in the upstroke, at pressures other than normal, or in the downstroke in head-on view, but such corrections proved insignificant in practice and were therefore omitted.

TABLE II

D. virilis: variation in components of stroke amplitude as a function of air pressure and density

Pressure in mm. Hg	3863	3087	2311	1520	760	380	190	95	
Density in gm. per L.	5.97	4.76	3.56	2.34	1.16	0.57	0.28	0.13	
	Displacement Relative to Frontal Plane in Degrees of Arc								Type of Record
Upstroke	72	77	76	79	86	93	94	93	Front view
Downstroke	−31	−33	−34	−34	−38	−40	−44	−45	Front view
Downstroke	−34	−38	−35	−34	−38	−39	−47	−43	Side view
	Displacement Relative to Transverse Plane in Degrees of Arc*								
Upstroke	−5	−1	−4	−3	−7	−6	−5	−5	Side view
Downstroke	20	20	29	22	29	28	25	27	Side view

Each datum is the mean of from 6 to 30 measurements.
* Negative values here indicate displacement in a posterior direction.

Angle YPA gives a measure of the true forward displacement of the costa at the conclusion of the downstroke. The vertical displacement may also be obtained from the same record by drawing the line through M and the intersection, E, with the horizontal, AB, of an arc of length PL centered at M. The angle MEP is then a measure of the actual depression of the costa below the horizontal. Average values for angle MEP were obtained in this way from records of 6 animals which flew at all pressures. As indicated in Table II, such calculated values are in substantial agreement with the mean values measured directly from head-on pictures of other flies.

RESULTS

Table I records the total vertical amplitudes measured from head-on records of 11 specimens which, with one exception, flew at all 8 pressures tested. From the same records, the displacement of the costa above and below the horizontal was determined separately; the averages of these values are shown in Table II, which includes for comparison the average downward displacements obtained

from 6 sets of records in side view (see the preceding section for the method of measurement). Also shown in Table II is the average angular displacement of the costa in the fore and aft direction at the conclusion of up- and downstroke, as determined from photographs taken in side view. Other alterations in the envelope of the wing movement in response to density change are illustrated by the series of silhouettes in Figure 3.

DISCUSSION

The data depict a significant trend toward greater amplitudes in the transverse plane at lower densities, and vice versa (Table I). When density is increased, both the upward and downward excursions of the wing are curtailed, while there is little change in the extreme fore and aft displacement of the wing (Table II). However, the trajectory of the wing varies in such a way as to give a broader envelope at lower densities when recorded in lateral view (Fig. 3).

The relationship between vertical displacement of the wing and density is linear on a double logarithmic scale, permitting calculation of the following regressions:

(a) limit of displacement above body axis (a_u) on density (ρ),

$$\log a_u = 1.9140 - 0.0885 (\log \rho - 0.2344); \tag{1}$$

(b) limit of displacement below body axis (a_d) on density (ρ),

$$\log a_d = 1.5688 - 0.0976 (\log \rho - 0.0944); \tag{2}$$

(c) total vertical amplitude (a) on density (ρ),

$$\log a = 2.0721 - 0.0934 (\log \rho - 0.2344). \tag{3}$$

In the calculation of equations (1) and (3), the empirical points at the lowest density, 0.13 gram per liter, were omitted, since they deviate significantly from the lines defined by the other observations. This discrepancy may be due to the fact that the upward displacement of the wing has already reached its physical limit, not greatly in excess of 90 degrees, at densities greater than 0.13 gram per liter. Another possibility is that performance at the lowest density was influenced to some extent by oxygen lack. In this series of experiments no attempt was made, as was done in the case of frequency (Chadwick and Williams, 1949), to rule out variation in oxygen tension and in total pressure as such as factors in the results obtained, since with the possible exception just noted, one sees no reason to suppose that either is implicated in the amplitude changes observed. But, in moist air at 27 degrees C. and at a density of 0.13 gram per liter the total pressure is 95 mm. Hg and the partial pressure of oxygen only some 15 mm., a value known to be close to the limit consistent with brief interrupted flight. It was frequently difficult to obtain a satisfactory response from the specimens at this pressure, and it is possible that those which flew were in a subnormal state. The remaining observations show but little scatter about the lines calculated, as judged by the chi-square test for dispersion. One may conclude then that amplitude is proportional, on the average, to the −0.09 power of density.

This finding may now be examined along the lines followed in the previous study of the dependence of wingbeat frequency on gas density.

$$P_o \propto mv^2f; \tag{4}$$

where P_o equals power output; m is the mass of air moved per stroke; v, the average velocity imparted to mass m; and f, wingbeat frequency.   Or

$$P_o \propto V_s\rho v^2f, \tag{4a}$$

since m equals $V_s\rho$, where V_s is stroke volume and ρ, air density.

Now, it is apparent that amplitude is a factor in both the stroke volume, V_s, and the velocity of the wing, v_w.   To the latter the air velocity, v, must, in turn, be proportional.   Consider that an approximation of the stroke volume, in terms of the wing dimensions, is given by regarding the volume swept out by the wing as the segment of a cylinder with radius equal to the wing length, L, and with height equal to the product of mean wing width, W, and the sine of the angle of attack, α.   Then

$$V_s \text{ (both wings)} = 2\pi L^2W \sin \alpha(2a/360°), \tag{5}$$

where a is the stroke amplitude.   For a similar calculation of the mean velocity imparted to the air, it is necessary to take account of the shape of the wing, which is narrowest at the base.   The mean velocity is therefore that produced by a unit area situated somewhat further than half the wing length from the articulation. Calling this radius L_m, we may then write

$$v \propto v_w \propto 2\pi L_m(2a/360°)f. \tag{6}$$

On substitution of expressions (5) and (6) for stroke volume and velocity, respectively, into equation (4a) above, one obtains:

$$P_o \propto a^3f^3\rho \sin \alpha. \tag{7}$$

Reference to the study by Chadwick and Williams (1949) shows that wingbeat frequency (f), for different individuals, varies on the average as the -0.09 power of density; that is, in the same quantitative manner as amplitude.   By substituting $\rho^{-0.09}$ for both amplitude (a) and frequency (f) in equation (7), one finds

$$P_o \propto \rho^{0.46} \sin \alpha. \tag{8}$$

Provided then that no further factor of importance has been overlooked, one may judge that equilibrium can be maintained under constant power output only by variation of $\sin \alpha$ as $\rho^{-0.46}$.

Reasons for supposing P_o constant, which were discussed fully in the previous publication, may be summarized as follows:

(a) P_o is equal to the product of power input, P_i, and an efficiency factor, e;

(b) P_i, measured in terms of oxygen consumption at different densities, is essentially constant;

(c) any factor which is to balance the relationship between frequency, amplitude, and density must show *continuous* exponential variation over the full range of densities investigated;

(d) a large increase in efficiency at higher densities, required if the relationship is to be balanced by alteration in P_o while P_i remains constant, is unlikely.

Although one is led by this reasoning to reject changes in efficiency as a plausible solution of the problem, it has been pointed out by O. Sotavalta (1947, 1951) that this treatment neglects energy losses due to inertia of the wing. These, he feels, may be considerable, inasmuch as the wing is reversing its direction of movement twice per cycle at frequencies of the order of 200 per second. Since there is appreciable variation in both frequency and amplitude, and hence, by inference, in rotational inertia of the wing, when density is altered, one must admit that the assumption of constant power output will be in error to the extent that efficiency is changed by variation in this loss. The possible significance of this factor in the flight of *D. virilis* may be assessed as follows:

$$E = 1/2 \, I(\omega)^2; \tag{9}$$

where E is the mean kinetic energy of rotation of the wing at any instant; I, the rotational inertia of the wing; and ω, its mean angular velocity, *i.e.*,

$$\omega = 2\pi(2a/360°)f. \tag{10}$$

Now,

$$I = m_w r^2, \tag{11}$$

where m_w is the mass of the wing and r the radius of gyration, which may be taken as approximating $\sqrt{1/L \int_0^L r^2 \cdot dr}$, or $L \times 3^{-0.5}$, L being the wing length.

If E is dissipated twice per stroke, the power loss per wing is $2fE$; per insect,

$$P_e = 4fE. \tag{12}$$

Combining equations (9), (10), (11) and (12) gives the solution (on substitution of the measured average values, for *D. virilis*, of 2×10^{-1} cm. for wing length, L, and 3.625×10^{-6} gram for wing weight, m_w):

$$P_e = 1.1784 \times 10^{-10} \text{ gm.cm.}^2 \times f^3 \times a^2. \tag{13}$$

From this equation, the values of P_e at different densities have been worked out, using our measurements of average f and a, and are given in Table III.

TABLE III

D. virilis: variation at different air densities of power loss due to inertia of wings

Density ρ grams per liter	Frequency* f cycles per second	Amplitude* a degrees of arc	Power Loss P_e ergs per second	Power Available for Useful Work P_0 ergs per second	$P_e/P_0 \times 100$ per cent
5.97	205	105	11.19	204.49	5.5
4.76	210	107	12.49	203.19	6.1
3.56	215	110	14.17	201.51	7.0
2.34	223	115	17.28	198.40	8.7
1.16 (1 atm.)	238	123	24.04	191.64	12.5
0.57	254	131	33.14	182.54	18.2
0.28	271	140	45.97	169.71	27.1
0.13	290	150	64.67	151.01	42.8

* Frequencies computed from data of Chadwick and Williams (1949); amplitudes, from equation (3) above; for full explanation of other calculations see text.

A figure for the *effective* power output at normal density, 25 degrees C., is available from unpublished data of Williams on *D. repleta*; the maximal value measured was 159.74 ergs per second.   Discounting the species difference, since *D. virilis* and *D. repleta* have approximately the same size and flight characteristics, and allowing for a measured frequency increase of 421 beats per minute per degree C. (since $P_o \propto f^3$), we can estimate the effective power output at normal density under the conditions of our present experiments at 191.64 ergs per second. If wing inertia, amounting to 24.04 ergs per second, is a complete loss, this would represent a total output of 215.68 ergs per second.   The fraction available for moving air at each density may now be calculated by subtracting from 215.68 ergs per second the corresponding calculated loss, P_e, due to inertia.   Thus we obtain the values shown in column 5 of Table III.   Two significant facts which emerge from these calculations are: (1) the power loss due to wing inertia in the flight of Drosophila probably does not exceed 45 per cent of the effective power output even under the most adverse conditions, and is normally much smaller than this; (2) although this loss varies in the proper manner, increasing at low densities and vice versa, and in proportion to $\rho^{-0.45}$, it is not of sufficient magnitude to provide balance in the relationship of equation (8) in the absence of variation in sin α.

A few additional comments are needed in reference to these calculations of the wing inertia.   The values derived above may be somewhat low, since the wing trajectory includes a varying horizontal component (see Fig. 3) not contained in our formula for the angular velocity.   Another inaccuracy stems from the fact that the true radius of gyration is, of course, unknown, though one doubts that it is greater than the length assigned, since the wing, though narrower, is appreciably more massive toward the base.   Granting that possibly somewhat higher estimates should be given for P_e than those shown in Table III, this error is counterbalanced to some extent by the probability that the value cited for the effective power output is low.   The figure quoted is merely the maximal output determined under a particular set of experimental conditions, and there is reason to believe that somewhat greater outputs might be measured with improved techniques. Finally, the assumption that the kinetic energy of the wing becomes a total loss, twice per cycle, is open to question.   A portion of this energy must be expended against the air and contribute useful work.   Although the larger fraction in each half cycle is dissipated, no doubt, in stretching the antagonistic sets of muscles, one must reckon also with the possibility, given the very short duration of the cycle, that a proportion of even this fraction is reabsorbed (cf. Hill, 1950).   Some energy may also be recaptured through elastic deformation of the thoracic cage. Weighing these various considerations together, it seems improbable that the actual loss of power due to wing inertia amounts to a fraction of the power output significantly greater than indicated in Table III.

We are thus left with a choice of assumptions: either the overall efficiency of flight varies, in some manner as yet unexplained, about as the -0.4 power of density, or the angle of attack of the wings on the air changes in the same proportion.   Believing that most animals are fairly well adjusted to their normal environment, one is reluctant to postulate increases of efficiency amounting to something over 100 per cent when Drosophila are placed in the wholly unnatural situation of being forced to fly at an air pressure of 5 atmospheres.   For this

reason the alternative, a comparable increase in the angle of attack at $\frac{1}{8}$ atmosphere and an equivalent reduction at 5 atmospheres, seems the more acceptable, although we regret our inability to settle the question experimentally. If, as suggested by the silhouettes of Figure 3, the quantity $V_s \rho v^2$ varies somewhat more rapidly with changing density than has been estimated on the basis of our measurements of frequency and vertical amplitude, the actual rate of variation required in the angle of attack may be even less than we have been led to postulate above. It is to be hoped that methods for attack upon the several unknowns still remaining in this problem will be developed.

The writer is indebted to Dr. C. M. Williams for valuable discussion in regard to all phases of this investigation.

Summary

The amplitude of wingbeat of *Drosophila virilis* Sturtevant in moist air at a temperature of 27 ± 1 degrees C. and at a series of gas pressures ranging from 3863 mm. Hg to 95 mm. Hg, was recorded photographically.

The vertical amplitude of the wingbeat decreased progressively with increase in air pressure. The excursion of the wing was curtailed in the same proportion at both extremes of the stroke. These changes are attributed to alterations in atmospheric density which resulted from the change in gas pressure. It is calculated that amplitude varies approximately as $\rho^{-0.09}$.

No significant change was observed in the limits of angular excursion of the wing in a fore and aft direction, although the envelope of the wing movement, as seen in lateral view, broadened as pressure was reduced.

It is shown that the measured changes in amplitude and frequency compensate only in part for the change in load which results from alterations in air density. The possible role of power losses due to wing inertia is discussed, and it is concluded that these represent only a minor factor in the observations. Arguments are presented which suggest that alterations in gas density provoke compensatory changes not only in wingbeat frequency and stroke amplitude, but also in the angle at which the wings attack the oncoming stream of air. The degree of compensation required would be provided by doubling the angle of attack at 95 mm. Hg and halving it at 3863 mm. Hg.

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